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Stability and Broad-Sense Heritability of Mineral Content in Potato: Calcium and Magnesium

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Abstract Calcium and magnesium are two minerals that play prominent roles in animal and plant metabolism. The purpose of this study was to determine if genetic variation exists among advanced potato breeding clones for tuber calcium and magnesium content and the extent of genotype x environment interactions on these two traits. Ten, 13, and 13 clones were evaluated in the Tri-State, Western Regional, and Western Regional Red/Specialty Trials, respectively. Tuber calcium content ranged from 266 to 944 μg-g^{-1} DW; magnesium from 787 to 1,089 μg-g^{-1} DW. Genotype x environment interactions were significant in all trials. However, only the Tri-State for calcium and the Western Regional Red/Specialty trials for both minerals displayed a significant source of variation for genotypes. Broad-sense heritabilities for tuber calcium content were 0.65, 0.37 and 0 in the Tri-State, Western Regional, and Western Regional Red/Specialty Trials, respectively. Broad-sense heritabilities for tuber magnesium content were 0.57, 0, and 0.72 in the Tri-State, Western Regional, and Western Regional Red/Specialty Trials, respectively. Potato is not a rich source of either calcium or magnesium for the human diet, but genetic variation exists among potato clones that might be useful for plant health.

Resumen El calcio y el magnesio son dos minerales que juegan papeles prominentes en el metabolismo de plantas y animales. El propósito de este estudio fue determinar si existe variación genética entre clones de papa avanzados para el contenido de calcio y magnesio en el tubérculo y el alcance de las interacciones genotipo x medio ambiente en estos dos caracteres. Se evaluaron 10, 13 y 13 clones de los ensayos de Tres-Estados, Regional del Oeste y Regional del Oeste Especialidad en Rojas, respectivamente. El contenido de calcio en el tubérculo varió de 266 a 944 μg por gramo de peso fresco; el de magnesio fue de 787 a 1,089 μg g-1DW. Las interacciones genotipo x medio ambiente fueron significativas en todos los ensayos. No obstante, solo las pruebas del Tres-Estados para calcio y la Regional del Oeste Especialidad en Rojas para ambos minerales exhibió una fuente significativa de variación para genotipos. Las heredabilidades en amplio sentido para el contenido de calcio del

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tubérculo fueron de 0.65, 0.37 y 0 para los ensayos de Tres-Estados, Regional del Oeste, y Regional del Oeste Especialidad en Rojas respectivamente. Las heredabilidades en amplio sentido para el contenido de magnesio en el tubérculo fueron de 0.57, 0 y 0.72, en los ensayos de Tres-Estados, Regional del Oeste y Regional del Oeste Especialidad en Rojas, respectivamente. La papa no es una fuente rica ni de calcio ni de magnesio para la dieta humana, pero existe variación genética entre los clones de papa que pudieran ser útiles para la sanidad de la planta.

Keywords Solanum tuberosum · Genotype x environment interaction · Breeding · ICAEPS · Biofortification

Introduction

Calcium is rarely deficient in soils but may present plant uptake problems on acidic soils. Vegetables may show quality reduction as a result of calcium disorders (Bangerth 1979). Ca deficiency may arise in the whole plant, or in a particular organ of the plant, but relatively little is known about the way in which Ca deficiency causes the observed symptoms. Typically, the symptoms of calcium deficiency, in addition to growth reduction, also comprise browning phenomena and, in severe cases, necrosis of whole areas of plant tissue. In contrast to other macronutrients, a high proportion of the total calcium in plant tissue is located in the cell wall (apoplast). The main known functions of Ca in the apoplast are to maintain the integrity of the plasmalemma and to stabilize the pectins both intra- and intermolecularly (White and Broadley 2003). Calcium levels in potato plants have been implicated in resistance to internal brown spot (Tzeng et al. 1986), heat necrosis (Yencho et al. 2008), and infection by the soft rot pathogen *Pectobacterium* spp. (McGuire and Kelman 1984), heat tolerance (Kleinhenz and Palta 2002), and freezing tolerance (Vega et al. 1996). Higher levels of calcium and magnesium in cooking water reduced sloughing (disintegration) when boiling tubers of the cultivar Russet Burbank (Zaehringer and Cunningham 1971). Although magnesium is rarely limiting to plant growth, several studies have shown a dramatic yield increase in potato with the addition of magnesium on deficient soils (Chucka 1934; Sawyer and Dallyn 1966). Magnesium is present in chlorophyll, is essential in allowing ATP to function and in activating many enzymes needed in photosynthesis, respiration and the formation of DNA and RNA (Wilkinson et al. 1990).

The range of variation and knowledge concerning the ratio of genetic variation to total phenotypic variation are useful in an assessment of the future prospects of taking potato from an insignificant source of calcium and magnesium to one that aids substantially in the alleviation of calcium or magnesium deficiency (Frossard et al. 2000). Neither calcium nor magnesium are thought to be particular crucial as macronutrients in human nutrition. Calcium is most often in a deficient status in the diet where populations do not have access to dairy products. The purpose of this study was to quantify variation of calcium and magnesium among advanced potato selections in several regional trials and to estimate broad-sense heritability, relating this to potato physiology and the human diet.

Materials and Methods

Field Experiments Potato genotypes in three distinct trials were planted at different locations in 2004. The 13 locations and associated crop management are described Brown et al. (2010; 2011). Each trial had a different array of genotypes. The Tri-state (TS) trials were comprised of four environments for each mineral, while the Western Regional Russet (WR) drew from 6 to 3 environments, for calcium and magnesium, respectively. The Western Specialty/Red Trials (W/SP/R) were grown in three environments for each mineral. Field trials were planted as randomized complete blocks, with four blocks. Plots consisted of 20 plants. Tubers were harvested mechanically and packaged out of the field and shipped to Prosser, WA. They were stored at 10 °C for 30 days at 85 % relative humidity. Three tubers from each plot were sliced, not peeled, dried, and ground to powder as a composite sample. Preparation of samples and analysis was described in Brown et al. (2010; 2011)

Statistical Analysis Calcium content was transformed to the natural logarithm for all statistical analyses and back-transformed for presentation of means. Magnesium values were not transformed. Variance components for each source of variation were estimated from the mixed models procedure in SAS (version 9.1, Cary, NC). Broad-sense heritability (H) was estimated as the ratio of the genotypic (σ^2_{G}) to total phenotypic variance, $\mathrm{H} = \sigma^2_{\mathrm{G}}/\left(\left(\sigma^2_{\mathrm{error}}/\mathrm{re}\right) + \left(\sigma^2_{\mathrm{GxE}}/\mathrm{e}\right) + \sigma^2_{\mathrm{G}}\right)$ (Holland et al. 2003), where r=number of replications and e=number of environments. Knapp et al. (1985) determined the exact confidence interval for H. The upper confidence interval is $1\text{-}[(\mathrm{MS}_1/\mathrm{MS}_2)\ \mathrm{F}_{(1\text{-}\alpha/2:\mathrm{df2,df1})}]^{-1}$, while the lower confidence interval is $1\text{-}[(\mathrm{MS}_1/\mathrm{MS}_2)\ \mathrm{F}_{(\alpha/2:\mathrm{df2,df1})}]^{-1}$, where MS_1=mean squares for genotype and MS_2=mean squares for genotype x environment. These mean squares were obtained from the type III mean squares from the general linear models procedure in SAS.

To evaluate the genetic stability of each potato genotype, the genotype x environment interaction (G x E) was partitioned into stability variance components (σ^2_{i}) assignable to each genotype (Shukla 1972), using a program written for the interactive matrix language procedure in SAS (Kang

Table 1 Calcium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the Tri-State trials

Genotype	TS-H[1]	TS-A[2]	TS-OE[3]	LT-OL[4]	Mean	σ_i^2	s_i^2
A95409-1	1,288	623	865	998	944	**	**
A96023-6	1,131	677	1,232	447	872	**	**
A96095-3	561	850	1,097	794	826		*
A96104-2	636	802	1,101	412	738		
A98295-3TE	562	651	987	248	612	*	
AO96164-1[a]	373	772	931	269	586	**	*
AOA95154-1[b]	367	607	930	274	545	*	
AOA95155-7	308	643	1,032	332	579	**	**
Russet Burbank	886	562	631	1,004	771	**	
Ranger Russet	910	644	628	360	636	*	**
Location mean	702	683	943	514			

*=P<0.05, **=P<0.01, significance level of variances σ_i^2, and s_i^2

[1] Hermiston, Oregon

[2] Aberdeen, Idaho

[3] Early harvest, Othello, Washington

[4] Late harvest, Othello, Washington

[a] Subsequently named 'Sage Russet'

[b] Subsequently named 'Clearwater Russet'

1989). An environmental index for each environment was calculated by subtracting the grand mean over all environments from the mean for each environment. Heterogeneity due to this index was removed from the G x E interaction and the remainder was partitioned into s_i^2 assignable to each potato genotype, and constitutes variance not explained by removal of environmental effects.

Results and Discussion

The analysis of the Tri-State trials included four environments in the Pacific Northwest, one in Aberdeen, ID, one in Hermiston, OR, and an early and late harvest in Othello, WA. Environments were not a significant source of variation for calcium, but G x E was. The stability analysis revealed that eight genotypes displayed significant G x E for calcium and six of these remained unstable after removal of environmental heterogeneity (Table 1). Both Russet Burbank and Ranger Russet, the most widely grown and the third most widely grown varieties in North America, respectively, displayed significant G x E and Ranger Russet remained unstable after environmental heterogeneity was removed. Magnesium content was analyzed over four environments. Genotypes and G x E were significant but environments were not. Four genotypes had significant G x E and three of these remained unstable after removal of environmental heterogeneity (Table 2). In addition, one genotype did not

Table 2 Magnesium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the Tri-State trials

Genotype	TS-H	TS-A	TS-OE	TS-OL	Genotype mean	σ_i^2	s_i^2
A95409-1	1,126	752	657	980	879	**	**
A96023-6	1,303	861	810	962	984	**	
A96095-3	1,070	968	780	920	935		
A96104-2	1,030	1,035	856	854	944	**	**
A98295-3TE	1,030	842	756	837	866		
AO96164-1	1,030	887	806	872	899		
AOA95154-1	976	877	817	748	855		**
AOA95155-7	1,118	1,092	783	1,074	1,017	**	**
Ranger Russet	946	864	697	769	819		
Russet Burbank	896	877	693	839	826		
Location mean	1,053	906	766	886			

*=P<0.05, **=P<0.01, significance level of variances σ_i^2, and s_i^2

Table 3 Calcium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the Western Regional Russet trial entries

Genotype	WR-K[1]	WR-S[2]	WR-EH[3]	WR-A[4]	WR-OE[5]	WR-OL[6]	Genotype mean	σ_i^2	s_i^2
A92030-5	528	627	475	493	232	691	508	**	**
A92294-6	447	508	300	328	241	371	366	**	**
A9304-3	342	695	381	539	212	377	424	*	
A9305-10[a]	354	629	480	453	317	419	442		
A93157-6LS[b]	578	746	749	603	245	662	597	**	**
A95109-1[c]	345	643	667	408	425	456	491	**	**
AC92009-4	378	772	1,038	536	272	539	589	**	**
AC93026-9	369	775	484	575	332	375	485	*	**
AO96160-3[d]	379	706	401	683	327	485	497	*	**
ATX92230-1	528	694	532	578	236	458	504		
CO93001-11	452	440	286	428	296	365	378	**	**
CO94035-15[e]	627	1,011	472	721	459	536	638	**	**
PA95A11-14	479	353	566	734	213	618	494	**	**
Location mean	447	661	525	545	293	489			

*=$P<0.05$, **=$P<0.01$, significance level of variances σ_i^2, and s_i^2

[1] Kimberly, Idaho

[2] Springlake, Texas

[3] Early harvest, Hermiston, Oregon

[4] Aberdeen, Idaho

[5] Early harvest, Othello, Washington

[6] Late harvest, Othello, Washington

[a/] Subsequently named ‘Alpine Russet’

[b/] Subsequently named ‘Premier Russet’

[c/] Subsequently named ‘Classic Russet’

[d/] Subsequently named ‘Owyhee Russet’

[e/] Subsequently named ‘Mesa Russet’

show significant G x E but had significant instability after removal of environmental heterogeneity. Magnesium content means over environments ranged from 766 to 1,053 μg-g^{-1} DW.

Table 4 Magnesium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the western regional Russet trials

Genotype	WR-EH[1]	WR-OE[2]	WR-OL[3]	Genotype mean	σ_i^2	s_i^2
A92030-5	1,319	703	869	964	**	**
A92294-6	885	798	688	790		
A9304-3	1,015	920	744	893		
A9305-10	959	948	773	893	*	*
A93157-6LS	1,074	862	816	917		
A95109-1	972	1,011	811	931	**	**
AC92009-4	1,015	789	755	853		
AC93026-9	966	897	705	856		*
AO96160-3	1,090	946	777	938		
ATX92230-1	1,118	796	877	930	**	**
CO93001-11	928	899	876	901	**	
CO94035-15	1,018	979	791	929	*	*
PA95A11-14	1,109	770	763	881	**	*
Location mean	1,036	871	788			

*=$P<0.05$, **=$P<0.01$, significance level of variances σ_i^2, and s_i^2

[1]Early harvest, Hermiston, Oregon

[2]Early harvest, Othello, Washington

[3]Late harvest, Othello, Washington

Table 5 Calcium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the Western Regional Red/Specialty Trials

Genotype	W/SP/R-H[1]	W/S/SP/R-A[2]	W/SP/R-M[3]	Genotype mean	σ_i^2	s_i^2
A96741-1R	448	444	301	398	**	
A96741-2R	440	524	254	406	*	*
AO93487-2R[a]	241	370	269	293	*	
All Blue	275	461	250	329		
BTX1544-2	260	530	212	334		
CO93037-6R	285	330	223	279	*	
CO94165-3[b]	154	452	191	266	**	**
CO94183-1[c]	233	375	347	318	**	**
NDA5507-3[d]	290	668	211	390	*	
VC0967-2	289	350	242	294		
VC1002-3	442	664	252	453		*
VC1015-7	328	665	229	407		
Yukon Gold	211	835	203	416	**	*
Location mean	300	513	245			

*=P<0.05, **=P<0.01, significance level of variances σ_i^2, and s_i^2

[1] Hermiston, Oregon

[2] Aberdeen, Idaho

[3] Mount Vernon, Washington

[a] Subsequently named 'Red Sunset'

[b] Subsequently named 'Purple Majesty'

[c] Subsequently named 'Mountain Rose'

[d] Subsequently named 'Yukon Gem'

The Western Regional Russet Trial was tested over six environments for calcium: two environments in Idaho, one in Texas, one in Oregon, and two in Washington. There were no significant differences among environments or genotypes, but the G x E interaction was significant. Eleven genotypes exhibited significant G x E and ten remained unstable after removal of environmental heterogeneity (Table 3). Data were obtained from three environments for magnesium. Neither genoytpes nor environments were significant, but G x E was. Seven genotypes showed significant G x E and six of

Table 6 Magnesium content (μg-g^{-1} DW) by trial location and overall, and significance of the contribution each genotype makes to G x E variance (σ_i^2), and residual (s_i^2) after removal of environmental heterogeneity in the Western Regional Red/Specialty Trials

Genotype	W/SP/R-H	W/SP/R-A	W/SP/R-M	Genotype mean	σ_i^2	s_i^2
A96741-1R	1015	1,064	717	932		
A96741-2R	1,149	1,294	825	1,089	**	*
AO93487-2R	1,065	1,222	778	1,022	**	*
All Blue	759	950	652	787	**	**
BTX1544-2	1,194	1,109	893	1,065		
CO93037-6R	860	796	733	796	**	
CO94165-3	886	886	678	817		
CO94183-1	1,091	1,020	840	984		
NDA5507-3	961	1,108	973	1,014	**	**
VC0967-2	1,165	1,138	772	1,025	**	
VC1002-3	1,007	920	812	913	*	
VC1015-7	1,210	1,092	697	1,000	**	
Yukon Gold	990	915	826	910	*	
Location mean	1,027	1,040	784			

*=P<0.05, **=P<0.01, significance level of variances σ_i^2, and s_i^2

these were unstable when environmental heterogeneity was removed (Table 4). In addition, one genotype did not show significant G x E but had significant instability after removal of environmental heterogeneity.

The Western Regional Red/Specialty trial was grown in three environments in the Pacific Northwest. For calcium, genotypes and G x E were significant, but environments were not. Eight genotypes showed significant G x E and five were unstable after removal of environmental heterogeneity (Table 5). Calcium content ranged from 266 to 453 μg-g^{-1} dry weight. Magnesium contents were likewise obtained from three environments. Genotypes and G x E were significant while environments were not. The mean over the three environments ranged from 787 to 1,089 micrograms per gram dry weight. Nine genotypes displayed significant G x E and four remained unstable after removal of environmental heterogeneity (Table 6).

Broad-Sense Heritability

Broad-sense heritability refers to the ratio of all genetic variation to total phenotypic variation. It is therefore not a predictor of expected gain from sexual breeding and selection, but rather a predictor of change effected by selection among the individuals in that population. Broad-sense heritabilities for calcium content and their 95 % confidence intervals were 0.65 (0.25, 0.88), 0.37 (−0.66, 0.88), and 0 for the Tri-State, Western Regional and Western Regional Red/Specialty Trials, respectively. Broad-sense heritabilities for magnesium content and their 95 % confidence intervals were 0.57 (0.14, 0.91), 0, and 0.72 (0.23, 0.90) for the Tri-State, Western Regional and Western Regional Red/Specialty Trials, respectively (Table 7). From these results it may be surmised that certain populations of breeding lines would increase in calcium and magnesium if selection were applied. Broad-sense heritability does not isolate additive genetic variance which would predict genetic gain due to intermating and selection. It is applicable to vegetatively propagated crops in the sense that, when significant, it predicts gain by selection within a group of genotypes that will not change genetically from this generation into the next. Gain in a selected subset is predicted to occur in proportion of the relative magnitude of the genetic variance versus total phenotypic variance. Selection among clones will result in highest gain where H is highest, e.g. for calcium among the Tri-State entries, and for magnesium among the Tri-State and Western Regional Red/Specialty trials. These breeding lines represent a small fraction of the total variation to be accessed in potato germplasm and a more thorough survey the Cultivated Collection of the International Potato Center or of wild accessions in the USDA/ARS Potato Germplasm Collection of Sturgeon Bay, Wisconsin, might provide a greater range to choose from. The calcium and magnesium contents are in conformity with a summary in Rastovski and van Es (1987). Andre et al. (2007) found calcium contents ranging from from 271 to 1,092 μg-g^{-1} DW in native South American cultivars. A study of wild tuber bearing species found levels of calcium ranging from 160 to 743 μg-g^{-1} under low calcium nutrient levels and from 474 to 1,829 μg-g^{-1} under high calcium levels in nutrient solution (Bamberg et al. 1993). In a follow-up survey, Bamberg et al. (1998) reported levels as high as 2,166, 2,168 and 2,121 μg-g^{-1} in specific selections of *S. kurtzianum*, *S. microdontum*, and *S. gourlayi*, respectively, under enhanced calcium fertilization. Casañas-Rivero et al. (2003) found that older varieties on the Canary Islands had higher values of calcium, but that this did not hold true for magnesium. *Chuño* is a dried potato product derived from bitter frost tolerant potatoes grown at high elevations in the Andes. The final product is a water-leached, freeze-dried food storable for long periods of time. The processing of *chuño* has been reported to increase calcium concentration by 25 % and decrease magnesium concentration by 75 % (de Haan et al. 2010). At present, in the US population, potatoes contribute 4.5 % of the magnesium in the diet (Subar et al. 1998). A 100 g FW portion of our highest calcium potato genotype (approx. 18 mg) would provide a male adult 2 % of the Recommended Daily Allowance (RDA). The same amount would constitute 2 % of the RDA for children 4 to 8 years. The same weight of potato provides 5 % percent of the RDA of magnesium for adult men and 15 % of RDA for infants 4 to 8 years old months (http://ods.od.nih.gov/factsheets/magnesium; http://ods.od.nih.gov/factsheets/calcium).

The daily requirements for macronutrients calcium and magnesium in the human diet are large compared to micronutrients iron and zinc. Even though potato contains much larger amounts of calcium and magnesium than of iron or zinc

Table 7 Broad-sense heritability (H) of calcium and magnesium content in the Tri-State, western regional Russet, and western regional red/specialty

	Tri-State	Western regional	Western regional red/specialty
Broad-sense heritability (H) Ca			
H	0.65	0.37	0
Upper CI	0.88	0.88	na
Lower CI	0.250	−0.66	na
Broad-sense heritability (H) Mg			
H	0.57	0	0.72
Upper CI	0.91	na	0.90
Lower CI	0.14	na	0.23

CI confidence interval

na not applicable

(Brown et al. 2010; Brown et al. 2011), it is not a rich source of either, because the RDA is high. Although it is likely that increases could be achieved by breeding it is doubtful that potato would ever be a considered an abundant source of either mineral in the diet. Common bean (*Phaseolus vulgaris*) has roughly ten times more calcium and magnesium than potato, for instance (Woolfe 1987). Calcium and magnesium contents may be of greater significance in the control of physiological disorders and diseases of potato and therefore may be more worthy of exploration at the high and low extremes of concentration of these two minerals with these objectives in mind.

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